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The Spruce Budworm, *Choristoneura fumiferana* (Clem.) and an Allied New Species on Pine (Lepidoptera: Tortricidae)[1]

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Introduction

This paper has been extracted mainly from the manuscript of a revision of the tortricid subfamily Archipinae, to make available a scientific name for an injurious, undescribed *Choristoneura* species that feeds in the larval stage upon pines, particularly jack pine, *Pinkus banksiana* Lamb., and red pine, *P. resinosa* Ait. This insect and the closely allied *Choristoneura fumiferana* Clem. are compared under the following topics: taxonomic history, maculation, morphology, and distribution. References are cited only if they contain information of taxonomic significance; the vast amount of economic literature dealing with these species has been omitted. This paper is followed by a comparative study of the larvae of the two species by Miss M. MacKay, by one by Miss C. E. Cox on the mathematical significance of the anatomical differences in the larvae and adults of both species, by a discussion of some of the parasites of the pine species by G. S. Walley, and by a discussion by S. G. Smith of the isolating mechanisms operating between the two species.

Taxonomic History and Discussion

The spruce budworm, *Choristoneura fumiferana*, was named by Clements in 1865 from specimens collected in Virginia. In 1890 Packard referred to the damage caused by the spruce budworm to the spruce and balsam in Maine during the latter part of the 19th century. Packard also included the following note, which was supplied him by the Reverend Elijah Kellogg: "According to Captain James Sinnet and Mr. John Jordan of Harpswell, the spruces of Harpswell and Oris Islands were destroyed in 1807. Captain Bishops, whose son made the statement to Mr. Kellogg, cut down the dead spruces on these islands and worked six weeks boiling the sea-water with fuel thus obtained, in order to make salt. This was during the embargo which led to the war of 1812 with Great Britain." Packard referred to this insect under the name *Tortrix fumiferana* Clem. In 1869 Robinson described the dark variants under the name *Tortrix nigridia* on the basis of specimens from Ohio, Pennsylvania, and Massachusetts. In 1913 Meyrick placed the species in the genus *Harmologa* Meyr., proposed by him for a group of primitive tortricid species from New Zealand. This placement was followed by Forbes in 1923. Since that time, the species has been assigned to either *Cacoecia* Hbn. or *Archips* Hbn. by various economic and taxonomic investigators. In 1947 Freeman placed the species in the genus *Choristoneura* Lederer, a combination currently used.

In 1935 Graham was the first to point out that the pine-feeding form was biologically distinct from the spruce-balsam form, and could be considered specifically distinct. In 1943 Brown and MacKay suggested that the two forms could be considered either specifically or subspecifically distinct and pointed out the differences in structure of the male genitalia. More recent unpublished

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taxonomic and biological investigations by various workers have shown that the two are specifically distinct.

The main differences are in wing pattern, ground colour of the fore wings, wing expanse, uncus width, food-plant preferences, and time of flight.

It should be noted that the two forms, which are dealt with in this paper, represent only a portion of the biological complex that comprises the coniferous-feeding forms of the genus *Choristoneura*. At present, knowledge and material are insufficient to show the relationship of the rest of the forms to one another, or to the two species under consideration. It is probable that outbreaks of these other forms have and do occur, but have been complacently considered as of *C. fumiferana* and so recorded. I mention them in the hope that forest entomologists may be aware of them and secure additional information that will assist in our understanding of their relationships.

A form, very closely related to the jack-pine species, occurs in Nova Scotia, and south through the Atlantic States to New Jersey. It is found where pine trees abound and has been reared from "*Pinus* sp.". It resembles the jack-pine species but lacks the silvery-white costal spots, and the dark transverse reticulations of the fore wings are much more prominent.

In the western United States and southern Alberta, several forms occur in association with pine. One of these, from southern Alberta, feeding on *Pinus contorta* Dougl., resembles the eastern jack-pine species but is smaller, has light fuscous hind wings, and has continuous light transverse bands on the fore wings. In Oregon, a form occurs on *Pinus lambertiana* Dougl. and was described by Busck as *Archips lambertiana*. The fore wings of this form have ocherous markings on a creamy ground colour. The hind wings are white. In Colorado, still another form occurs on *Pinus ponderosa* Laws. This moth has dark ocherous fore wings with a few lead-coloured spots and a creamy-white costa. The hind wings are light fuscous. In California and Arizona there exist two more closely allied forms, which have been described as *Archips retiniana* Wlshm. and *Archips carnana* B. & Bsk. The food plants of these are unknown to me, but it is possible that they are pine feeders. All these forms, no doubt, are entities of several cryptic species and are not to be confused with the spruce-balsam-Douglas fir complex that occurs in the same areas. It appears impossible to ascertain the taxonomic status of these cryptic forms by a morphological appreach. The relationships and taxonomic status can only be ascertained by a biological study of their behaviour in nature, supplemented by experiments to determine food-plant preferences and other biological characteristics.

Choristoneura pinus* n. sp.

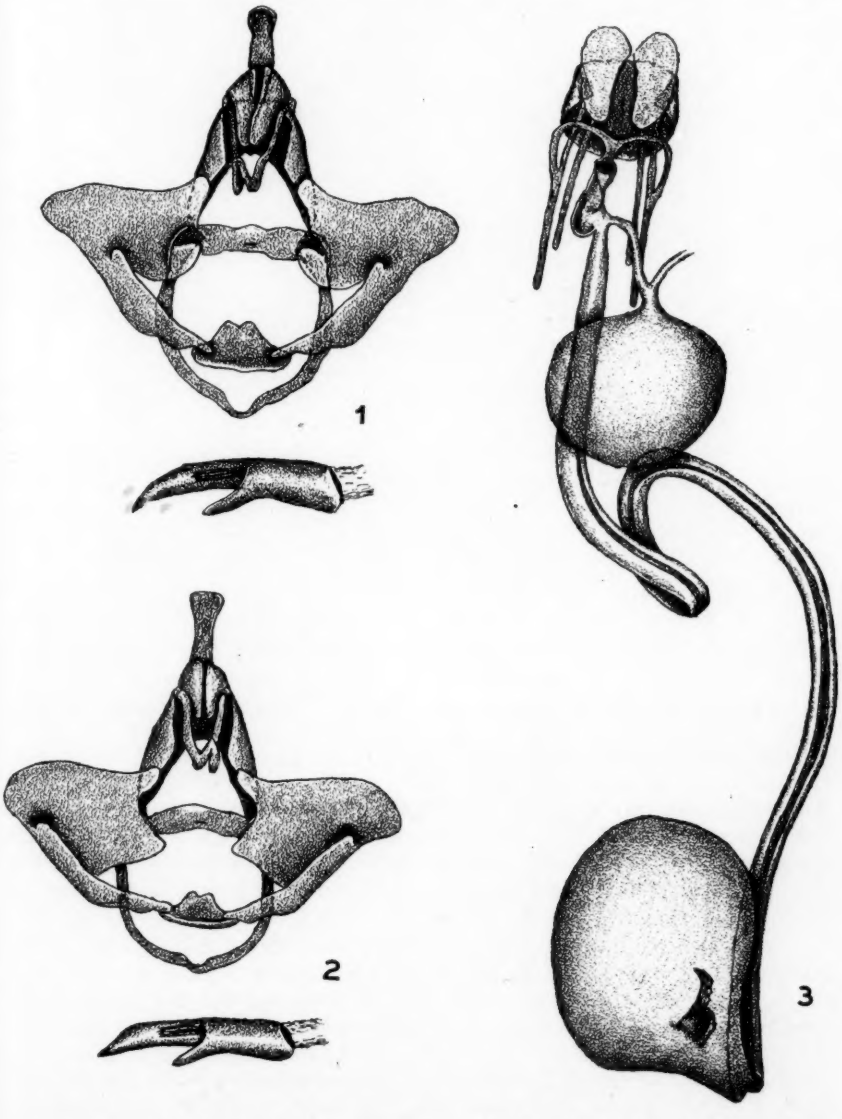
Figs. 17-22

Archips fumiferana (Clem.) in part; Graham, 1929. Papers Michigan Acad. Sci. Arts and Letters 9 (1928): 517-523; 1929, Principles of Forest Entomology, p. 147, McGraw-Hill Book Company, New York; 1935, Univ. Michigan School For. Bull. 6; 1939, McGraw-Hill Book Company, New York. Brown and MacKay, 1943, Canadian Ent. 75: 207.

Male.—Head ocherous-tawny. Palpus concolorous, with the apical segment fuscous. Thorax and fore wing ocherous-tawny, the latter with distinct maculation consisting of ocherous-tawny basal patch, median band, and outer streak, separated from one another by silvery or ocherous-white areas and sprinkled with short, transverse striae of darker scales. The basal patch well defined outwardly, extending from the basal fourth of the costa to just beyond the middle of the hind margin, indented below the cell and extending along the hind margin to a point in line with the costal portion. Median band constricted in the cell by a concavity of the inner margin; extending rather broadly and irregularly to

*The name *Choristoneura pinus* was inadvertently validated by G. B. Oakland (1953. *Can. Ent.* 85: 109). Application is being made to the International Commission on Zoological Nomenclature for the suppression, for nomenclatorial purposes, of the trivial name *pinus* in Oakland's paper.

the posterior margin, its outer margin reaching the tornus. Apically from the median band, a silvery-white, quadrate costal spot, is finely connected to a silvery, irregular area that extends to the tornus. Beyond, toward the apex, a large, dark costal spot is more or less connected to a concolorous ovate spot below. Apical region concolorous with the light areas of the wing and containing a subapical series of darker dots. The lighter area between the basal patch and the median band tending to whitish on the posterior margin. The costa containing



Figs. 1-3. 1, Male genitalia of *C. pinus* n. sp. 2, Male genitalia of *C. fumiferana* Clem. 3, Female genitalia of *C. pinus* n. sp.

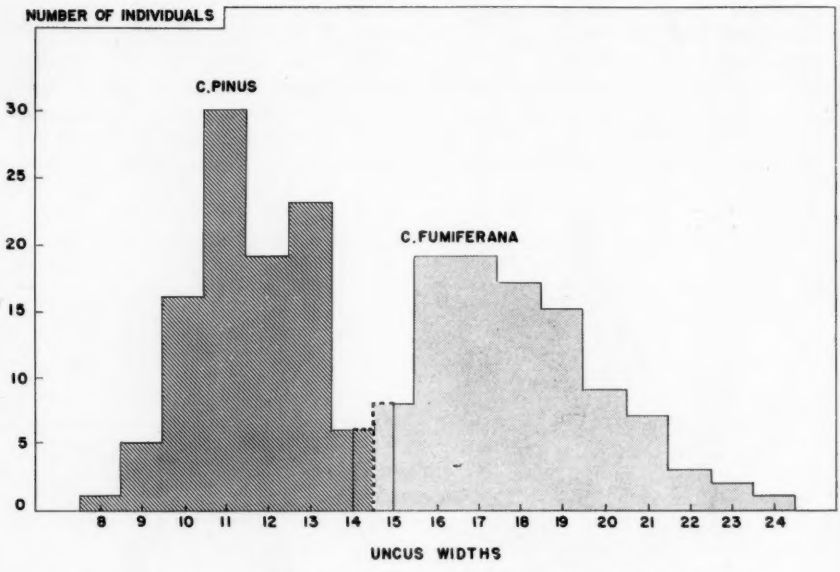


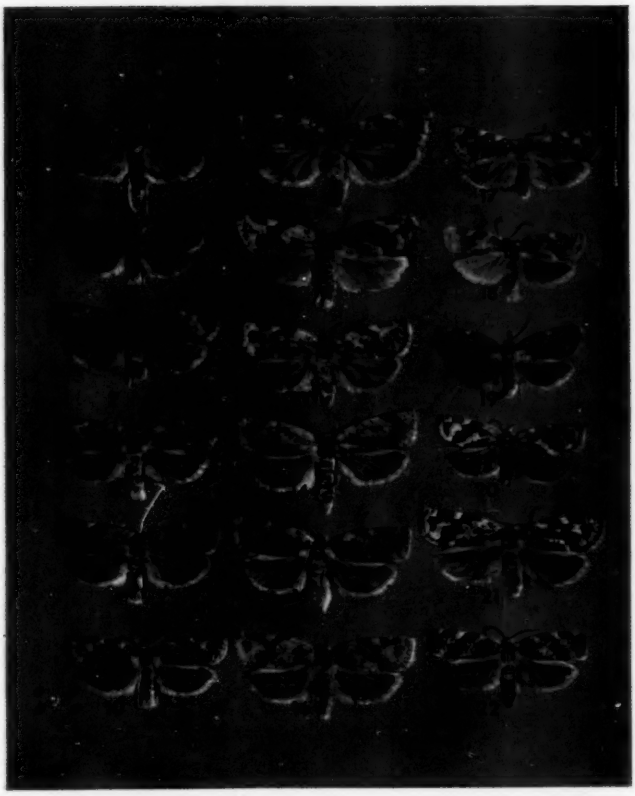
Fig. 4. Uncus widths of *C. pinus* and *C. fumiferana;* one unit=10.53 microns.

two or three fine, white subapical streaks. Fringe shining fuscous. Hind wing entirely dark smoky with a white fringe marked by a dark basal line. Undersurfaces of all wings fuscous, that of the fore wing lighter on the costa with the white costal spot repeated below and with darker costal streaks; hind wing beneath, lighter along the costa and with ocherous-tawny apical spots.

Female.–Similar to the male but often with the lighter bands more silvery-white. Expanse of holotype male, 20.5 mm.; male paratypes, 18-23 mm.; female paratypes, 15-24 mm. Moth in July, flying approximately two weeks later than *fumiferana.*

The maculation of *C. pinus* is rather uniform within the species as compared with that of *fumiferana.* Fig. 17 represents a typical male and Fig. 21 a typically marked female. These two specimens show the typical ocherous-tawny ground colour. In a few specimens (Figs. 18, ♂, and 20, ♀) the ocher colour predominates in the fore wings, the specimens are darker, and the maculation is less distinctive. The hind wings of most of the specimens are dark fuscous but approximately one specimen in 150 has one hind wing considerably lighter (Fig. 18). In general, the smaller size, the ocherous-tawny ground colour, and the silvery-white costal spot distinguish *pinus* from *fumiferana.*

Male Genitalia (Fig. 1).–Typical of the genus. Claspers broad with narrow sacculus heavily sclerotized, folded and terminating in a blunt tooth at outer third. Aedoeagus broad, with ventral terminal tooth and four deciduous cornuti. Socii well developed, pendulous. Transtilla a simple broad band. Uncus with apex spatulate or narrowly spoon-shaped, apex narrower than that of *fumiferana,* varying in width from 94.77 microns to 147.42, distribution being bimodal with peaks at 115.83 and at 136.89 microns. The uncus widths of the two species (Fig. 4) appear to abut one another in the region between 14 and 15 units, though not to overlap. The largest measurement for *pinus* was 14 units and the smallest



Figs. 5-22. 5-10, *Choristoneura fumiferana* Clem. Males. Ottawa district. 11-16, *Choristoneura fumiferana* Clem. Females. Ottawa district. 17-19, *Choristoneura pinus* n. sp. Paratypes. Males. Beauséjour, Manitoba. 20-22, *Choristoneura pinus* n. sp. Paratypes. Females. Beauséjour, Manitoba.

for *fumiferana* was 15, as indicated by the solid lines at 14 and 15; the dotted lines indicate the remaining portions of the class width.

Female Genitalia (Fig. 3).—Typical of the genus. Ductus bursae extremely long with a thin, longitudinal sclerotized band extending from the neck of the bursa to near the ostium. Neck of the ostium inclined. Dorsal ostial plate narrow. Signum in bursa shaped like a curved horn with a bulbous base.

Holotype.—Male, Beauséjour, Manitoba, July 21, 1951 (V. Hildahl). No. 5684 in the Canadian National Collection, Ottawa.

Paratypes.—200 males and 164 females, Beauséjour, Manitoba, July 13-23, 1951. No. 5684 in the Canadian National Collection, Ottawa.

Food Plants.—Pinus spp., especially *banksiana* Lamb. and *resinosa* Ait. Rarely spruce, *Picea* spp.

Distribution.—Nova Scotia, Ontario, Manitoba, Michigan. It seems probable that the total distributional pattern of *pinus* is unknown. No material has been seen from the jack-pine area west of Manitoba and north of the prairie region. I have seen material only from Nova Scotia, Ontario, and Manitoba. Through-

out most of its known distributional range, it is sympatric with *fumiferana*, flying about two weeks later.

Remarks.—This species is easily distinguished by the ocherous-tawny colour of the fore wing with the distinct banding. It is remarkably uniform in colour and size, being generally smaller than *fumiferana* Clem.

***Choristoneura fumiferana* Clemens**

Figs. 5-16

Tortrix? fumiferana Clemens, 1865, Proc. Ent. Soc. Philadelphia 5: 139.
Tortrix nigridia Robinson, 1869, Trans. Am. Ent. Soc. 2: 268, pl. 4, fig. 20, ♂.
Tortrix fumiferana Clem., Packard, 1890, Fifth Rept. U.S. Ent. Comm., p. 830; Fernald, 1902, *In* Dyar's List N.A. Lep. No. 5406, p. 483.
The Spruce-bud *Tortrix*, Packard, 1884, Am. Nat., p. 424.
Harmologa fumiferana Clemens, Meyrick, 1913, Gen. Insect. Fasc. 149, p. 41: Forbes, 1923, Cornell Univ. Agr. Expt. Sta. Mem.: 68, 489.
Archips fumiferana Clemens, in part: Graham, 1929, Papers Michigan Acad. Sci. Arts and Letters 9 (1928): 517-523; 1929, Principles of Forest Entomology, p. 147, McGraw-Hill Book Company, New York; 1935, Univ. Michigan School For. Bull. 6; 1939, Principles of Forest Entomology, p. 174, McGraw-Hill Book Company, New York. McDunnough, 1939. Check List Lep. Can. & U.S.A., Pt. 2, p. 57; Brown and MacKay, 1943, Canadian Ent. 75: 207; Freeman, 1946, Ann. Rept. Ent. Soc. Ontario, 1945, p. 8.
Cacoecia fumiferana Clemens, Atwood, 1944, Can. Ent. 75: 64.
Choristoneura fumiferana Clemens, Freeman, 1947, Can. Ent. 79: 21; 1948, Ent. News 59; 202; 1949, Can. Ent. 81: 10.

Maculation extremely variable. Fore wings mottled, and with suffused, indistinct bands rather than the usual basal patch, median band, and outer costal spot. Rarely in some individuals the median band rather well defined. Head and thorax usually grey, sometimes reddish-brown. Fore wing usually grey (Figs. 5-9, 11-13) with suffused, indistinct darker markings and short striae. Rarely some males (Fig. 10) and more commonly the females (Figs. 14-16) with a reddish cast approaching the colour of *pinus* but lacking the distinct maculation of the latter. The basal patch indistinct, usually represented by a few indistinct, blackish striae. The area of the median band, as a rule, more uniformly coloured than the rest of the wing and the median band usually distinct only on the costa. *The middle of the wing, as a rule, containing a blackish spot or bar, above which is a whitish costal spot.* Beyond the middle of the wing, a whitish or more usually greyish area, often with the veins outlined with darker scales. The region of the outer costal spot more or less connected to the tornus by a dark streak. The apical region of the wing lighter with a few dark speckles. Fringe shining, light fuscous. Hind wing uniformly dark fuscous with whitish fringe containing a dark basal line. Undersurfaces of all wings shining fuscous, the fore wing darker with light and dark costal spots, the hind wing lighter fuscous with lighter apex containing a few dark spots.

Expanse.—Males 21-26 mm.; females 22-30 mm. Moth in late June and early July, flying approximately two weeks earlier than *pinus*.

Throughout the range there is a large amount of intra-specific variation in maculation and pigmentation, but there is no evidence of discontinuous variation of a geographic or subspecific nature. The more frequent variation in the amount of red colouring that replaces the fuscous is more commonly associated with the females and gradually increases in frequency from east to west. It may be considered as a partially sex-associated character with an east-west clinal frequency.

Male Genitalia (Fig. 2).—Uncus constricted before apex; wider at apex than in *pinus*, varying from 155.3 to 252.72 microns. Otherwise similar to that of *pinus*, differences in the two drawings of the genitalia being due to the different positions of the slide mounts from which they were made.

Female Genitalia.—Similar to those of *pinus*.

Type Locality.—Virginia.

Type.—Acad. Nat. Sci. Philadelphia.

Food Plants.—Spruce and balsam, more rarely larch and pine.

Distribution.—Essentially a moth of the boreal forest. From Virginia north to Labrador, west across Canada and the northern United States to British Columbia, south in the Cordilleran region to Arizona and California, and north to the Yukon.

Although I have included the Cordilleran region in the distribution of *fumiferana*, it is possible that in this region there are one or more cryptic species. There is insufficient information on the biology of the Cordilleran population to present a clear taxonomic treatment of the budworms of that region. The eastern spruce-balsam population may represent two cryptic, sympatric species, one on spruce and one on balsam. However, there is no evidence to support such a contention and outbreaks of the budworm occur on both plants simultaneously if both plants are present in the area.

Summary

That portion of the Boreal forest of North America east of the prairies contains two major pest species of the genus *Choristoneura*, namely, *C. fumiferana* Clemens, which feeds on balsam and spruce, and *C. pinus* n. sp., which feeds on pine. Their main differences are tabulated below:—

	C. fumiferana	*C. pinus*
Ground colour	Usually grey, rarely ocherous-tawny	Ocherous-tawny, never grey
Wing pattern	Usually indistinct	Distinct
	Small black spot or bar usually present near middle of fore wing	No such black spot or bar
	Light costal spots dull white or grey	Light costal spots silvery white
Wing expanse	21-30 mm.	15-24 mm.
Food plants	Balsam and spruce, rarely larch and pine	Pines, particularly jack and red, rarely spruce
Width of subapical portion of uncus	155.3-252.72 microns	94.77-147.42 microns
Moth emergence	Two weeks earlier than *pinus*	Two weeks later than *fumiferana*

The Larvae of *Choristoneura fumiferana* (Clem.) and *C. pinus* Free. (Lepidoptera: Tortricidae)[1]

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Introduction

It has long been known that a series of late-instar larvae of *Choristoneura fumiferana* (Clem.) may be distinguished from one of *C. pinus* Free. by colour differences of the head and prothoracic shield: specimens of the former usually have dark heads and light prothoracic shields; specimens of the latter usually have light heads and dark prothoracic shields. However, intensive study of the larvae, including numerous specimens of *C. fumiferana* from the spruce-balsam fir areas of Algonquin Park, Ontario, and of *C. pinus* from jack-pine areas at Normandale, Ontario, has shown that there are highly significant structural differences in the head; these differences serve to identify small series of either species and most single specimens.

Descriptions of the larvae of both species, and a short discussion of their differences, are given herein. The systems followed in naming the setae are those of Fracker (1915) and Heinrich (1916).

Choristoneura fumiferana (Clem.)

Second Instar.—Average head length: 0.53 mm.; average head width: 0.65 mm.; average length of median dorsal line from anterior edge of postclypeus to termination of adfrontal sutures: 0.40 mm.; average width of postclypeus: 0.30 mm. Head and shield usually dark brown; body whitish. Integument with papillae very large and very few in number compared with those of later instars. Mandible lacking small tooth at base of first tooth, which is usually apparent in late-instar larvae.

Ultimate Instar (Figs. 1 & 7).—Average length: 20 to 22 mm.; average length of head: 1.52 mm.; average width of head: 1.82 mm. Integument (cf. Fig. 3) densely spinulated; spinules short, stout, and dark; minute papillae on which spinules are set heavily pigmented in dark areas of body, much less so in light areas. Dorsum and ventrum dark brown, spiracular and subspiracular areas brownish-yellow; colouring of body due to pigmentation of papillae; setal bases, except those of prothorax, on slightly raised yellowish areas, which are conspicuous on dorsum and ventrum. Setae moderately long. Spiracles circular, dark-rimmed, pale-centred.

Head (cf. Figs. 12 & 13) usually dark brown, overlaid with an almost black pattern; some specimens with a dark-brown pattern on a tan ground colour. Anterior seta 2 (A_2) about equidistant from A_1 and A_3, and at the apex of a triangle formed by these three setae. Ocellus II equidistant from ocelli I and III, that distance being more or less equal to its diameter. Lateral seta (L_1) farther from ocellar seta 2 (O_2) than from A_3. Average length (Fig. 7) of median dorsal line from anterior edge of postclypeus posteriorly to termination of adfrontal sutures: 1.17 mm.; average width of postclypeus: 0.81 mm.

Median longitudinal width of postclypeus more or less equal to that of preclypeus. Width of labrum about one and three-quarters times length; sides of notch on anterior margin forming an angle of 106° to 130° (18 specimens measured).

Mandible (cf. Fig. 11) with five teeth, the first three large and sharply pointed, the fourth smaller but pointed, the fifth straight-edged; internal ridges

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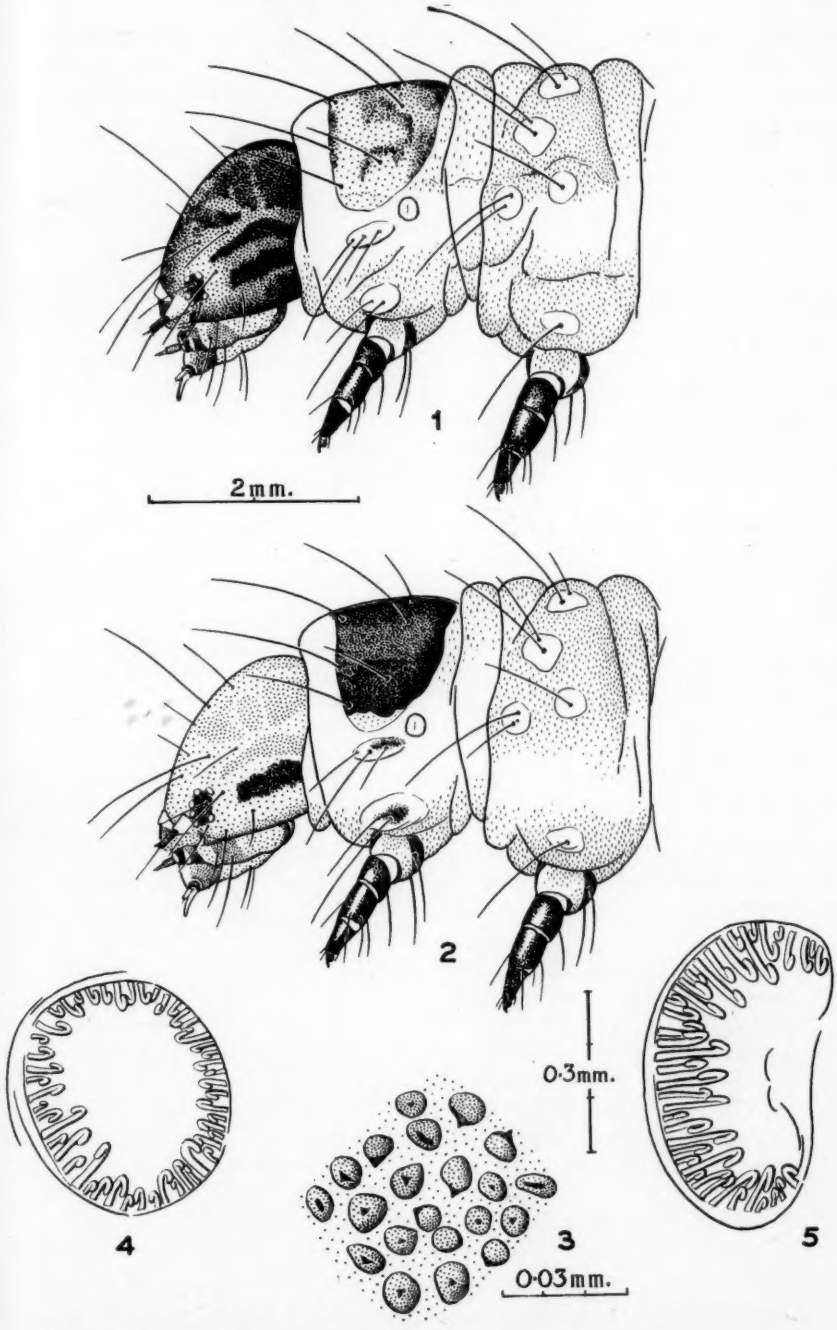
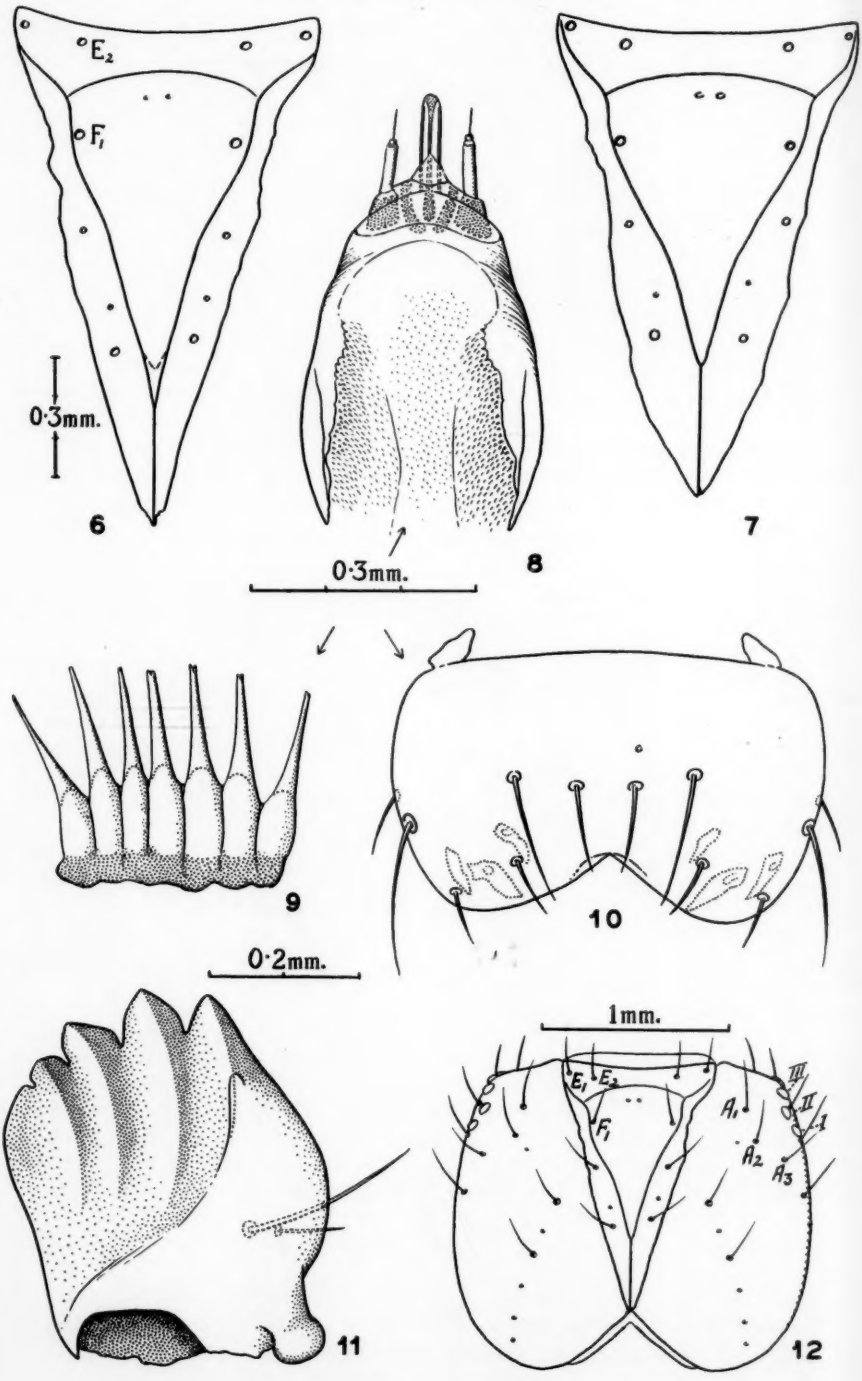


Fig. 1. *C. fumiferana* (Clem.). Head, prothorax, mesothorax.

Figs. 2-5. *C. pinus* Free. 2, head, prothorax, mesothorax; 3, integument highly magnified, showing spinules; 4, crotchets of left ventral proleg of sixth abdominal segment; 5, crotchets of left anal proleg.


E2
F1
0·3mm.
6
0·3mm.
8
7
9
10
0·2mm.
1mm.
E1
E2
F1
A1
A2
A3
III
II
I
11
12

from ocellar seta 2 (O_2) than from A_3. Average length (Fig. 7) of median from first tooth, at base of latter, a small tooth, sometimes difficult to observe.

Spinneret (cf. Fig. 8) rounded at tip; as long as or longer than labial palps, length approximately four and one-half to five times width. Free margin of blade of maxillula edged anteriorly with about six or seven very small, tooth-like processes; lobes clothed with small spines; gorge armed with minute spines, which are often scarcely discernible under high magnification, and limits of gorge itself usually difficult to define.

Prothoracic shield sclerotized, yellowish with some diffusion of dark-brown pigment; some specimens with considerable dark-brown pigment. Prothoracic Kappa and Pi setal groups on raised sclerotized areas, yellowish in colour with seldom any dark-brown pigmentation; middle seta of Kappa group ventrad of or in horizontal line with other two.

Pi group of setae (cf. Fig. 14) on mesothorax and metathorax unisetose, on seventh abdominal segment tristetose, on eighth abdominal segment bisetose.

Anal shield sclerotized, yellowish in colour. Prongs of anal fork (cf. Fig. 9) variable in number but most commonly six, seven, or eight; bases stout; tips needle-like or more often furcate.

Thoracic legs dark brown. Ventral and anal prolegs light in colour; proleg shields sclerotized but not conspicuous; crotchets (cf. Figs. 4 & 5) uniserial, biordinal; crotchets of ventral proleg of sixth abdominal segment 45 to 60, those of anal proleg 30 to 50 in number.

***Choristoneura pinus* Free.**

Ultimate Instar (Figs. 2-6, 8-13).—Average length: 20 to 22 mm.; average length of head: 1.70 mm.; average width of head: 1.93 mm. Integument (Fig. 3), colour, and colour pattern of body as in *C. fumiferana*.

Head (Figs. 12 & 13) usually brownish-yellow, overlaid with a slightly darker pattern, and with lateral bar and ocellar area dark brown, almost black; some specimens with a dark-brown pattern on a tan ground colour. Anterior setae and ocelli as in *C. fumiferana*. Average length (Fig. 6) of median dorsal line from anterior edge of postclypeus posteriorly to termination of adfrontal sutures: 1.34 mm.; average width of postclypeus: 0.84 mm. Width of labrum (Fig. 10) as in *C. fumiferana*, but sides of notch on anterior margin forming an angle of 80° to 115° (28 specimens measured).

Mandible (Fig. 11) as in *C. fumiferana*.

Hyphopharynx (Fig. 8) as in *C. fumiferana*, but a possible tendency for spinneret to average slightly more in length than that of *C. fumiferana*.

Prothoracic shield usually dark brown, almost black; some specimens with considerable yellowish pigment. Prothoracic Kappa and Pi setal groups on raised sclerotized areas, yellowish, with usually some dark-brown pigmentation.

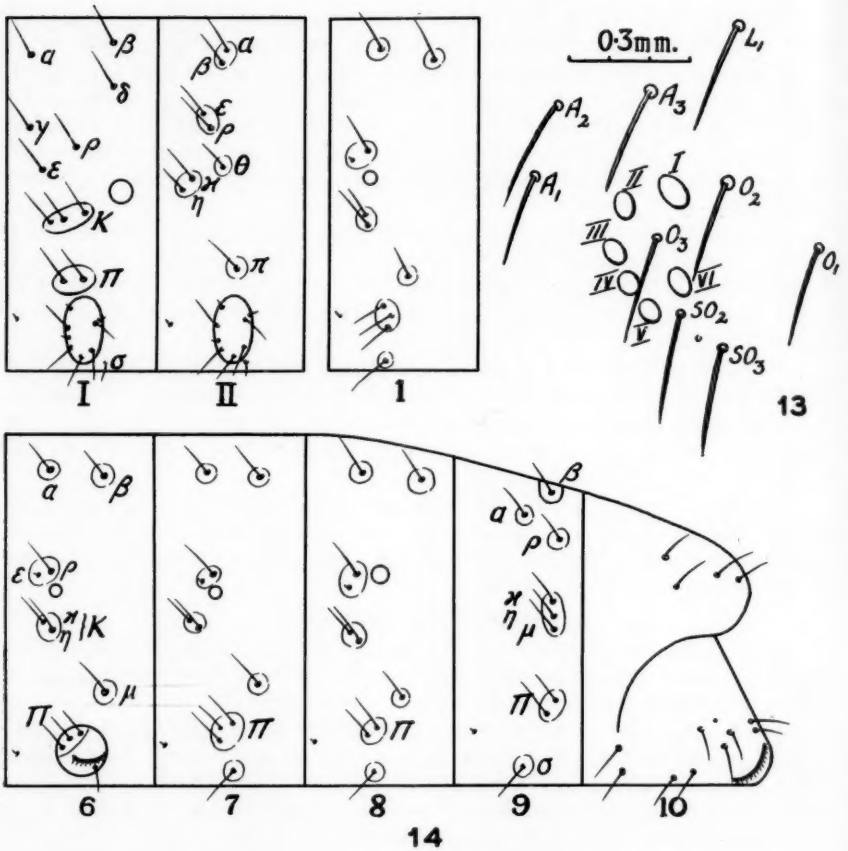
Setae of thoracic and abdominal segments (Fig. 14) as in *C. fumiferana*.

Anal shield sclerotized, yellowish, often with dark-brown pigmentation posteriorly. Anal fork (Fig. 9) as in *C. fumiferana*.

Thoracic legs, prolegs, and crotchets of prolegs (Figs. 4 & 5) as in *C. fumiferana*.

Figs. 6, 8-12. *C. pinus*. 6, postclypeal, frontal, and adfrontal areas; 8, hypopharynx, spinneret, and labial palp; 9, anal fork ventral view; 10, labrum; 11, mandible; 12, setal map of head capsule.

Fig. 7. *C. fumiferana*. Postclypeal, frontal, and adfrontal areas.



Figs. 13, 14. *C pinus*. 13, relative positions of ocelli and surrounding setae; 14, setal maps of first and second thoracic segments and 1st, 6th, 7th, 8th, 9th, and 10th abdominal segments.

Discussion of Differences

It is apparent that even in such closely related species as *C. fumiferana* and *C. pinus* there may be sufficient structural and colour characteristics to distinguish the larvae of one species from the other.

In the above species the structural differences occur entirely in the head. The head capsule of *C. pinus* is usually larger than that of *C. fumiferana*, and its length in relation to its width greater, similarly the length of the median dorsal line from the anterior edge of the postclypeus to the termination of the adfrontals in relation to the width of the postclypeus.

Measurements were made of the length and width of the heads of 75 last instar specimens of *C. fumiferana*: the width divided by the length averaged 1.20 within a range of 1.13 to 1.25. The same measurements were made of 34 late instar specimens of *C. pinus*: the width divided by the length averaged 1.13, but within a range of 1.05 to 1.30 with 18 of the specimens falling in the *fumiferana* range.

Measurements of the width of the postclypeus and of the length of the median dorsal line from the anterior edge of the postclypeus to the termination of the adfrontals were found to be more constant. I have, therefore, designated the latter divided by the former as the *postclypeal index*. The postclypeal index for 51 last instar specimens of *C. fumiferana* averaged 1.46 within a range of 1.40 to 1.54, and for 73 last instar specimens of *C. pinus* 1.58 within a range of 1.50 to 1.70, with about 20 per cent of each species falling between 1.50 and 1.54. Student's *t* test showed these means to be significantly different at the one per cent level.

Corresponding to the proportionately narrower postclypeus of *C. pinus*, the distances between the frontal setae (F_1) and between the epistomal setae (E_2) average slightly less than in *C. fumiferana* (Figs. 6 & 7). No other setal differences were noticed on the head capsule.

The tendency toward a deeper notch on the anterior margin of the labrum, and a spinneret with a possibly longer average length are other characteristics not at all incompatible with the longer head structures of *C. pinus*.

Several dozen specimens of second-instar larvae of *C. fumiferana* and a few third and fourth instars of both species were also studied. Early instars of *C. fumiferana* and *C. pinus* have heads and prothoracic shields of about the same colour, so that such specimens cannot be identified by colour differences. Measurements were made of the width and length of the heads of 18 specimens of second instar larvae of *C. fumiferana*: the width divided by the length averaged 1.24 within a range of 1.14 to 1.39. The postclypeal index of 21 specimens averaged 1.35 within a range of 1.23 to 1.46. The differences between the postclypeal indices and the head measurements not only agreed with those of late instar larvae of their respective species, but indicated a possibly greater divergence in average postclypeal indices. It seems probable, therefore, that these measurements are useful in all stages with the possible exception of the first instar, which to date has not been studied, and that further study of earlier instars may prove the postclypeal index more reliable for early than for late instars.

Accurate measurements of the width of the postclypeus were difficult to obtain in second-instar larvae, even in specimens that had been in KOH solution. However, it is preferable to use the postclypeal index, where possible, for identification, and other measurements only as a check in doubtful specimens.

Acknowledgments

I wish to thank Dr. S. G. Smith and Mr. G. A. Bradley of the Forest Insect laboratories at Sault Ste. Marie and Indian Head respectively for their kindness in supplying larval material and host and locality information.

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Morphological Differences Between the Pupae and the Egg Clusters of *Choristoneura fumiferana* (Clem.) and *C. pinus* Free. (Lepidoptera: Tortricidae)[1]

By I. M. CAMPBELL[2]

During the course of genetic studies on the spruce and jack pine budworms, it was noted that there are distinct morphological characters on which the pupae and egg clusters may be separated. They are described here as a contribution towards the taxonomic separation of *Choristoneura fumiferana* (Clem.) and *C. pinus* Free.

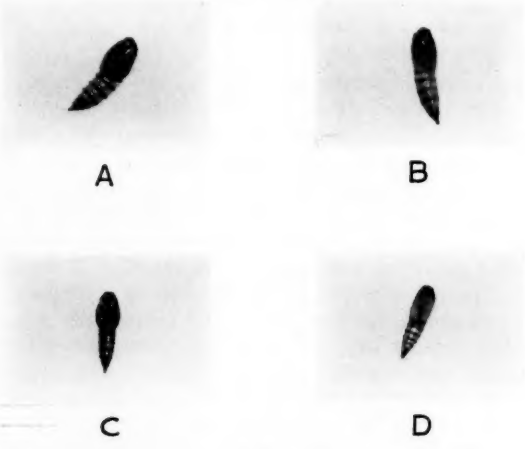

FIG. 1

Pupae of *C. fumiferana* and *C. pinus* before wing-scale formation:
(A) *C. fumiferana* ♀;
(B) *C. pinus* ♀;
(C) *C. fumiferana* ♂;
(D) *C. pinus* ♂.
Kodachromes by D. R. Wallace; slightly enlarged.

	C. fumiferana	*C. pinus*
Wing pad shape.	Strongly convex when viewed from above or below.	Flat or feebly convex when viewed from above or below.
Wing pad colour.	Initially yellowish to blue-green, due to haemolymph colour. Pigmentation between veins rapidly increasing with age. Ultimate colour, after formation of wing scales, dark-brown to dark-grey. No colour difference between the sexes.	*Males*: Initially yellowish. *Females*: Initially and invariably green, untinged by yellow or blue. No pigment concentration between veins. After scale formation, the sex difference becomes obliterated. Ultimate colour red-brown.
Abdominal segment colour.	Dark-grey to dark-brown.	Yellow to red-brown.
Pigmentation pattern on abdominal segments.	Distinct.	Faint or absent.

Experience has shown that these differences, once recognized, allow with high accuracy the immediate separation of the two species, and, in the case of *C. pinus*, the two sexes.

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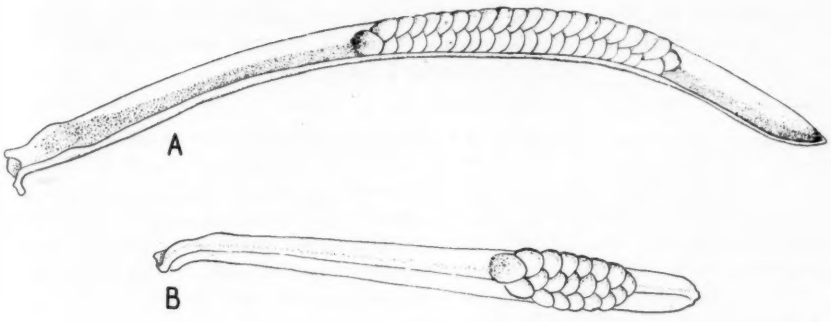

FIG. 2
Typical egg clusters of: (A) *C. pinus* on jack-pine needle; (B) *C. fumiferana* on balsam-fir needle.

	C. fumiferana	*C. pinus*
Number of rows of eggs	2 to 4, often variable within clusters	Always 2
Average number of eggs per cluster	19	37
Preferred host	Balsam fir and spruce	Jack pine

Graham (1935) found that the two species have a pronounced tendency to oviposit on their preferred host trees under laboratory conditions.

Table I shows the mean size of *C. pinus* clusters to be approximately twice the size of those of *C. fumiferana*. In 1947, females of each were allowed to oviposit on both balsam fir and jack pine to test the possibility that cluster size may be determined by the different needle lengths of the two species. The resulting means did not indicate striking effects attributable to needle length, but were statistically inconclusive owing to unforeseen inadequacies in the technique: the experiment will therefore have to be repeated.

TABLE I
Mean number of eggs per cluster in *C. fumiferana* and *C. pinus*

	C. fumiferana		*C. pinus*	
Year	No. of clusters	Mean ± S.E.	No. of clusters	Mean ± S.E.
1947	218	20.35 ± 0.76	123	31.57 ± 1.90
1948	233	18.45 ± 0.82	20	40.85 ± 5.57
1949	292	19.19 ± 0.68	97	40.51 ± 3.15
1950	194	19.18 ± 0.81	141	38.91 ± 2.22

It is worth noting that the difference between the two species in the number of eggs per cluster is not a direct result of differences in fecundity: actually fecundity is dependent more on the number of clusters deposited. Other things being equal, the size of the egg cluster varies inversely with the number of clusters laid.

Analysis of Frequency Distribution of Adults and Larvae of *Choristoneura fumiferana* (Clem.) and *C. pinus* Free. (Lepidoptera: Tortricidae)[1]

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A rapid means of identifying species of insects on the basis of physical measurements is useful to the field worker. The efficiency of the postclypeal index in separating the larvae of two closely allied species is illustrated herein. Occasionally species fall into overlapping subgroups, making it difficult to determine the characteristics of a given subgroup. A method useful in identifying such subgroups is outlined herein.

Use of Postclypeal Index

The width of the postclypeus and the length of the median dorsal line from the anterior margin of the postclypeus to the termination of the adfrontal sutures (to be called length) were measured for 68 last-instar specimens of *Choristoneura pinus* Free, and 51 last-instar specimens of *Choristoneura fumiferana* (Clem.). These measurements were used in the form of the postclypeal index, L/W, as a rapid means of separating the two species of larvae.

To determine the efficiency of this index the variance and the correlation of the widths and the lengths were determined for each specis. Variance, range, mean, and fiducial limits of the mean were determined for the postclypeal index of each species. The following statistics were obtained:—

	C. pinus	*C. fumiferana*
Variance of width	.1366	.0697
Variance of length	.2963	.1490
Variance of index	.0020	.0016
Correlation coefficient	.9279	.8802
Range of the index	1.49—1.70	1.37—1.52
Mean of the index	1.59	1.47
Fiducial limits of index mean	±.014	±.015

The variance is low for both length and width and of the same order for both species. The correlation coefficient is high in both cases, indicating a close relationship between length and width. The fiducial limits for the index means do not overlap and Student's t test showed the means to be significantly different at the one per cent level.

Six specimens, or 8.8 per cent of the sample of *C. pinus*, and 11 specimens, or 21.5 per cent of the sample of *C. fumiferana*, lay within the range overlap. An overlap as high as 20 per cent indicates that the postclypeal index is not an accurate means of differentiating between the species. However, the index may be sufficiently accurate for general purposes and those larvae occurring within the overlap region may be set aside for more critical examination.

Graphical examination of the data indicated a linear trend. A linear discriminant function (Hoel, 1947, pp. 121-126) of the type $z=aX+bY$ was fitted, where X and Y are the length and width respectively and z is a number characteristic of each larva and thus of the species. The equation so fitted was

$$z=X-1.1782Y.$$

Analysis of z in the same manner as for the postclypeal index gave the following statistics:—

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	C. pinus	*C. fumiferana*
Variance of z	.0469	.0342
Range of z	1.58—2.49	0.99—1.72
Mean of z	2.03	1.34
Fiducial limits of z mean	±.068	±.068

The means of the discriminant function for the two species were significantly different at the one per cent level. Five specimens, or 7.4 per cent of the sample of *C. pinus*, and 5 specimens, or 9.8 per cent of the sample of *C. fumiferana*, lay within the range overlap. The overlap for both species is of the same order and not greater than 10 per cent. Therefore the discriminant function technique of separation of the two species is more accurate than that of the postclypeal index.

For practical purposes the postclypeal index is sufficiently accurate as a means of rapid separation of the two species of larvae. The discriminant function is not so rapid but is more accurate and may be applied when a sharper means of separation is required.

It must be noted that these means and functions were obtained on the basis of last-instar larvae though the latter were a representative sample of the species as a whole. It is possible that other instars of these species have their own characteristic indices and discriminant functions.

Use of Probability Paper

The frequency distribution of the uncus widths of 100 adult males of each species was examined by means of probability paper. The histogram for these had indicated that *C. pinus* was bimodal and *C. fumiferana* unimodal (Freeman, 195 , Fig. 4). The larval measurements were also examined by means of probability paper for the possibility of polymodality.

Harding (1949) dealt with the use of probability paper for separating polymodal frequency distributions in biological problems. Probability paper had been in use for some years but its application to biological problems was new. It may be used to estimate the means and the standard deviations of the groups or populations that are separable and also give an estimate of the fraction of each one present in the sample. A slide rule is sufficiently accurate for the necessary calculations in plotting.

Briefly, the method is one of plotting the cumulative percentage frequency in the sample and drawing a line or lines that will have as a resultant a curve closely approximating the original cumulative percentage frequency curve. If the cumulative percentage curve is a straight line, then the sample is of a single, normally distributed population or group (unimodal). If the cumulative percentage frequency curve is sigmoid (one point of inflexion), then the sample is of two overlapping, normally distributed populations or groups (bimodal). Sigmoidal curves (two or more points of inflexion) are descriptive of three or more overlapping, normally distributed populations or groups.

Inspection of the cumulative percentage frequency curve yields an approximation of the proportionate distributions of the populations or groups present. The point or points of inflexion indicate the approximate line or lines of division. They are not as accurate in the central region because of the nature of probability paper, and the lines describing each population or group must be adjusted to the point of best fit. This is necessary as there are often only two or three points to define one of the lines, and the variation is such that there is a wide choice of slopes. Choose the one that best describes the data.

A certain amount of adjustment must be made when grouping the original frequencies. The size of the groups is fairly important. If the class interval is

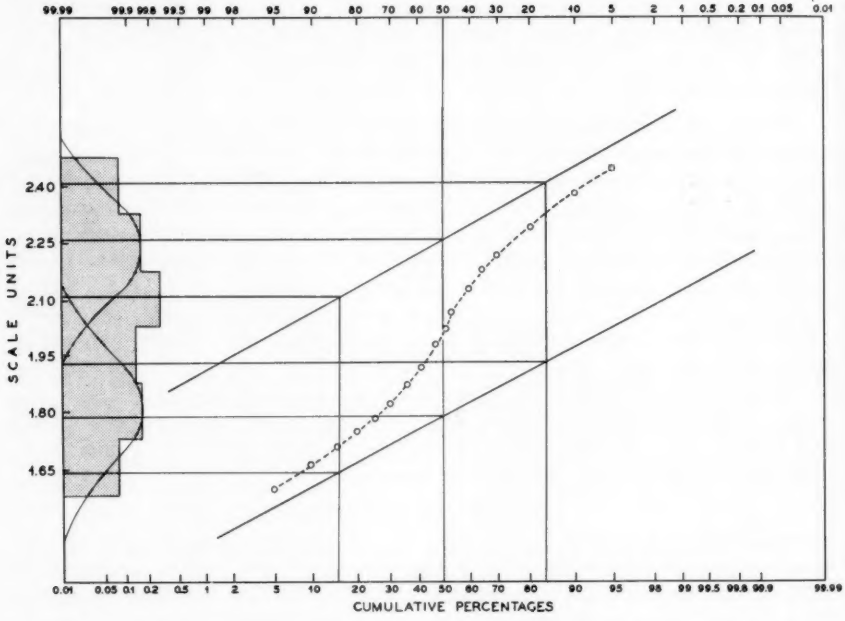

Fig. 1. Cumulative percentage frequency curve for discriminant function of *C. pinus.*

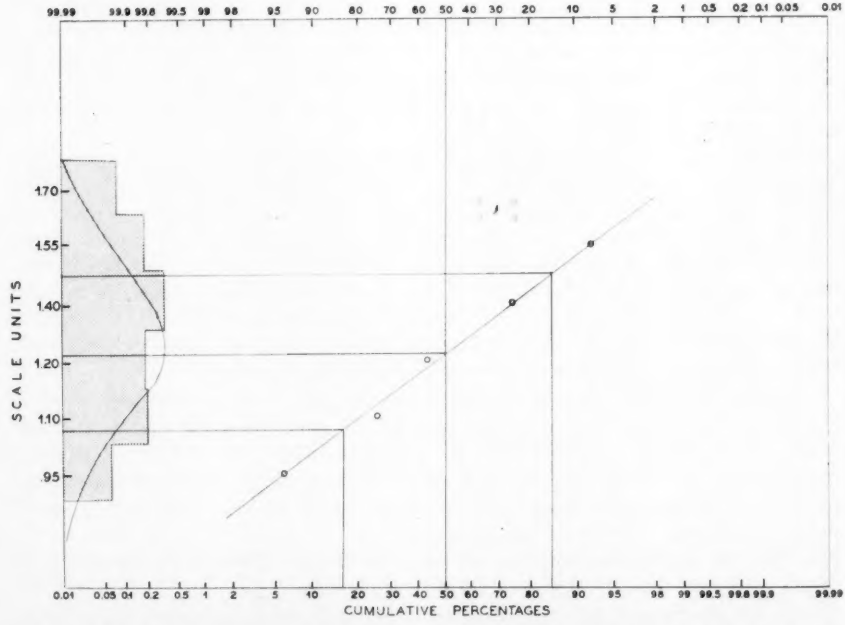

Fig. 2. Cumulative percentage frequency curve for discriminant function of *C. fumiferana.*

too small, a large number of excessively small values or zeros will apear in the frequency table and interfere with the fitting of the normal curve and also necessitate a large amount of grouping within the frequency table. Grouping is more difficult with a small number of frequencies than with, say, 200 to 500 or more.

Species Subgroups

Larvae.—Initially the lengths and postclypeal widths of the larvae were examined separately for each species. Fitting the cumulative percentage frequency curves showed that *C. pinus* was bimodal and *C. fumiferana* was unimodal. The point of inflexion was somewhere between 40 and 60 per cent for *C. pinus*.

To separate the groups in *C. pinus*, the group of smaller measurement was taken as A and that of larger measurement as B. Resultant cumulative percentage frequency curves were determined where group A was assumed to be 40 per cent, 50 per cent, and 60 per cent of the sample. Means and standard deviations for A and B were determined and normal curves fitted by areas. The χ^2 test of goodness of fit was applied to the theoretical distribution to determine which fraction most closely approximates the observed values. The possibility of *C. pinus* being unimodal was also examined and the fit of the normal distribution tested. Groups A and B were present in equal proportions for the width measurements, whereas group A was present in 60 per cent of the sample for the length measurement. This suggested some discontinuity and some means of using the two measurements together was sought. The linear discriminant function, combining length and width measurements made of the larvae of each species to determine a single representative number, z, seemed appropriate. The values of z were examined (Fig. 1) in the same manner as the original measurements and the χ^2 test made on the fit of the normal distribution obtained from them.

The cumulative percentage frequency curve of z for *C. pinus* showed groups A and B present in equal proportions (Fig. 1). The dotted line between the two solid lines is the resultant. The cumulative percentage frequency curve for *C. fumiferana* showed unimodality for both length and width; similarly, the cumulative percentage frequency curve of z was unimodal (Fig. 2).

Adults.—The uncus widths of 100 adult males of each species were examined for polymodality. In this case the chances of extra variation or hidden points of inflexion were fewer as the sample consisted of males only. The larvae presumably being males and females in equal numbers, sexual differences may have introduced a bimodal effect.

The cumulative percentage frequency curve for uncus width of *C. fumiferana* was linear, indicating a unimodal group (Fig. 3). That for *C. pinus* was sigmoid, and the χ^2 test of goodness of fit showed groups A and B present in equal proportions (Fig. 4).

Figs. 1 to 4 are based on microscope eyepiece scale units. By converting the data to millimetres and microns the following means and standard deviations were determined from the graphs for each species:—

Species	Character	Mean	S.D.
C. fumiferana	postclypeus width	1.16 mm.	.10 mm.
	length	1.68 mm.	.09 mm.
	uncus width	181 μ	27 μ

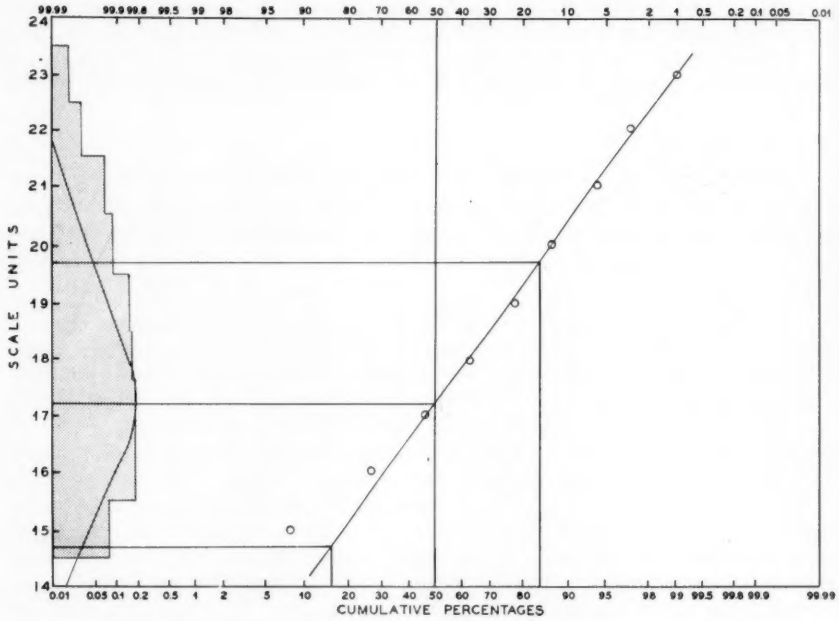

Fig. 3. Cumulative percentage frequency curve for uncus widths of *C. fumiferana.*

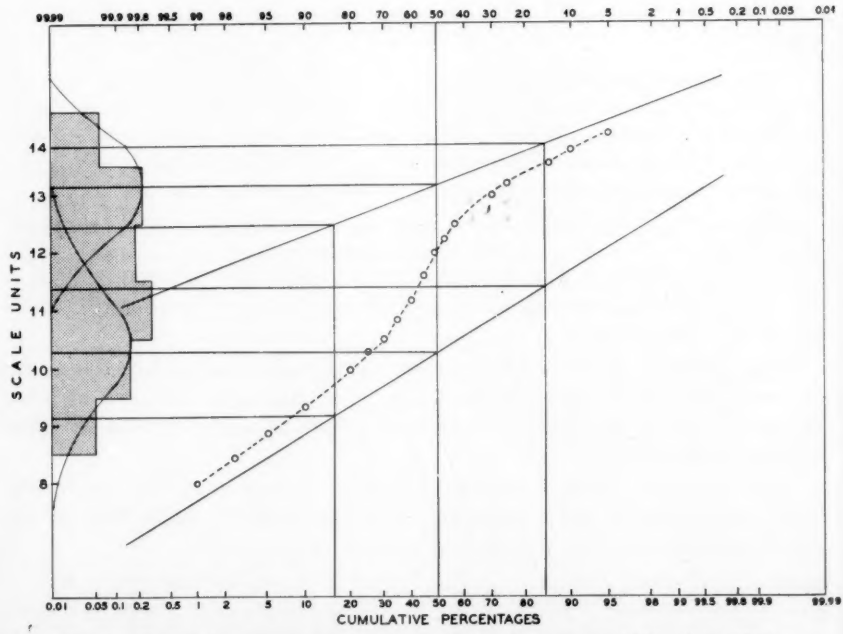

Fig. 4. Cumulative percentage frequency curves for uncus widths of *C. pinus.*

C. pinus	postclypeus width		
	group A	1.15 mm.	.05 mm.
	group B	1.36 mm.	.06 mm.
	length		
	group A	1.82 mm.	.07 mm.
	group B	2.12 mm.	.07 mm.
	uncus width		
	group A	108 μ	12 μ
	group B	139 μ	7 μ

Acknowledgments

I wish to thank Dr. T. N. Freeman, Systematic Entomology, Division of Entomology, and Miss Margaret R. MacKay, Division of Forest Biology, Science Service, who kindly made the foregoing data available.

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Reproductive Isolation and the Integrity of Two Sympatric Species of *Choristoneura* (Lepidoptera: Tortricidae)[1]

By STANLEY G. SMITH[2]

Introduction

According to Dobzhansky (1951a, p. 262) "Species are . . . groups of populations the gene exchange between which is limited or prevented by one, or by a combination of several, reproductive isolating mechanisms". This definition follows from his concept of a species not as a static unit but as a stage in the process of evolutionary divergence. Limitation or prevention of gene exchange is a property of geographic and reproductive isolation (Mayr, 1942), the various types of which Dobzhansky lists as follows:

I. Geographic or Spatial Isolation
II. Reproductive Isolation
  A. Ecological Isolation
  B. Seasonal or Temporal Isolation
  C. Sexual, Psychological or Ethnological Isolation
  D. Mechanical Isolation
  E. Gametic Isolation
  F. Hybrid Inviability
  G. Hybrid Sterility
  H. Hybrid Breakdown

Several of these have been shown to be effective in various degrees, individually in limiting the interchange of genes between, and collectively in maintaining the integrity of, *Choristoneura fumiferana* (Clem.) and *C. pinus* Free. The factual data that have been accumulated in measuring to what extent the various mechanisms contribute to complete isolation are too numerous to be detailed here: they will therefore only be summarized at present, but will be given at length in a future series of papers.

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Observations

Geographic isolation: Because so little is known concerning the constitution of the budworms populating the Rocky Mountains and the Prairie Provinces, it is at present appropriate to discuss in general terms the two species of *Choristoneura* only in relation to their distribution in Canada, east of the western border of Ontario.

C. pinus is virtually restricted in feeding to jack pine, *Pinus banksiana* Lamb., occurring on other conifers rarely and then only when they are growing in conjunction with jack pine. *C. fumiferana* is less discriminating, feeding broadly on balsam fir, *Abies balsamea* (L.) Mill., white spruce, *Picea glauca* (Moench) Voss, black spruce, *Picea mariana* (Mill.) B.S.P., and to some extent on tamarack, *Larix laricina* (Du Roi) K. Koch.[3] In so far as their host trees have a common geographic distribution, the two species are therefore sympatric; but, since *C. pinus* has rarely been recorded in Canada as occurring, for example, east of southern Ontario, in some regions they are in fact allopatric. Their maintenance as distinct species *throughout their range* is therefore not due to geographic isolation; it is attributable to genetically determined reproductive isolation. So far as has been determined this comprises a number of components, the total of which, even without the reinforcement of geographic isolation, successfully prevents hybridization between the two species, but none of which alone is perhaps entirely effective. These will be reviewed in the following paragraphs.

Ecological isolation: As feeding larvae, the species are largely restricted to their preferred hosts, upon which pupation subsequently occurs. Virgin females are more or less incapable of active flight (Wellington, 1948) and as a consequence are at first anchored to the host tree, upon which, following mating, they deposit at least some of their eggs. The males are under no such handicap and in areas of common occurrence are therefore, theoretically at least, free to indulge in promiscuous copulation. Field observation, however, points to the host preferences shown during larval stages being retained at maturity, for adults are rarely found on other than their host trees. Further field observation likewise indicates an absolute preference in oviposition site, and confirmation is provided by correlating egg clusters, which with some degree of assurance can be recognized as to species, with tree species in samples of field collected foliage.

There is considerable evidence that both species are subject to varying degrees of passive dispersal by air currents immediately following hatching and again after emergence from over-wintering. The apparent absence of heavy populations on other than their individual complexes of preferred hosts, however, implies extensive mortality and/or secondary migration conditioned by 'misplacement'. It seems logical to conclude then, that, since both passive larval dispersal and active adult migration (see later) can serve to bring populations of the two species into close propinquity, in areas of common occurrence, ecological isolation must play an important contributory part in preventing introgression of foreign genes.

Temporal isolation: In areas of overlapping distribution, where alone the two species can be strictly compared, the majority of representatives of the two are found to reach the adult stage at different times of the year: temporal isolation is thus essentially complete. Observational data recorded at the Wabigoon River in the Kenora District of Ontario, in 1948, and at nearby McIntosh Road, during 1949, are tabulated for *C. fumiferana* and *C. pinus* in Table I.

[3]See Brown and MacKay (1943) for a brief statement on host tree relationships.

TABLE I

Adult eclosion dates for the two sexes of *C. fumiferana* and *C. pinus:* data from Wabigoon River, 1948 and McIntosh Road, 1949

Species	Sex	First	Peak	Last
C. fumiferana	♂	28–6–48	4–7–48	12–7–48
	♀	1–7–48	4–7–48	13–7–48
C. pinus	♂	14–7–48	16–7–48	24–7–48
	♀	15–7–48	18–7–48	28–7–48
C. fumiferana	♂	2–7–49	4–7–49	10–7–49
	♀	3–7–49	5–7–49	10–7–49
C. pinus	♂	11–7–49	15–7–49	23–7–49
	♀	12–7–49	17–7–49	26–7–49

Field, insectary, and laboratory observations have individually and collectively demonstrated that the specificity of the different eclosion times shown in Table I is genetically determined, partly through species differences in time of emergence of larvae from diapause (see Table II) and partly through species differences in tempo of subsequent development. Temporal isolation in this instance is thus a composite in which are included what might be termed phenological and ontogenetic isolation.

Temporal isolation is obviously by far the most effective mechanism operating against introgressive hybridization in areas of common occupation, for at the most only a minute fraction of the two populations occur together as adults at one and the same time. The observations on flight periods recorded at McIntosh Road in 1949, however, clearly admit of the possibility, remote though it be, of a limited amount of hybridization. This possibility is considerably enhanced by the demonstration of a pronounced correlation between sex and the rate of development in both species (Table VII): under insectary conditions males predate females in eclosion by two or more days, depending on species. Such a difference in areas of overlap might conceivably result in virgin *C. fumi-*

TABLE II

Mean number of days delay in emergence from diapause by species and sex*: Sault Ste. Marie, 1951

Species	No. ♀♀	Mean	No. ♂♂	Mean	Mean ♀+♂	Diff.
C. fumiferana	77	7.90	71	8.04	8.00	5.44
C. pinus	103	13.81	143	13.17	13.44	

*Incubated at 72°F., and a relative humidity fluctuating between 70 and 100%; the estimated differential at the Wabigoon River in 1948 was 8–9 days.

ferana females coexisting with freshly emerged *C. pinus* males[4]. Yet hybrids appear not to materialize: extensive sampling of adults at both the Wabigoon River and McIntosh Road investigation sites failed to reveal the presence of hybrids, despite the fact that, on the basis of artificial, laboratory-conducted experiments, such hybrids are known to be phenotypically distinct and thus readily recognisable. Clearly an additional factor is operative in preventing their realization. It should be mentioned in this connection that a breakdown of temporal isolation owing to mass flight appears not to be an extreme hazard, since it is probable that all the females involved will already have been inseminated, as is evidenced by their flight, and that the males that have remained unmated will to some extent be repelled by the alien females (see under sexual isolation).

Sexual isolation: The importance of this barrier to an exchange of genes via those representatives of the two species that have chanced to circumvent the earlier-mentioned isolating mechanisms has been measured over a number of years by a variety of "mate-choice tests", which have provided tolerably consistent results. The most extensive series involved caging together equal numbers of both sexes of the two species and, by simple observation (copulation lasts some four hours–Table VI), determining the frequencies of the four possible types of matings. The combined results of these experiments are given in Table III, together with the chi-square value for deviation from equality and the index of sexual isolation. This latter value is computed from the number of intra-specific

TABLE III

The measurement of sexual isolation between the two species of *Choristoneura*

	f♀ x f♂	f♀ x p♂	p♀ x f♂	p♀ x p♂	Chi χ^2	P	ISS
Exp.	36	36	36	36			
Obs.	73	16	10	45	70.16	$<.01$	+.64

minus the number of inter-specific matings over the total number observed: it can therefore range from +1.0, where isolation is complete, through zero, where no selection is expressed, to –1.0, where the populations tested exhibit an absolute preference for cross-mating–minus values are perhaps by and large attributable to the artificial conditions that inhere in the experimental method.

In the tests involving *C. fumiferana* and *C. pinus*, the limitation operating against random exchanges between the respective genotypes is clearly of major proportion, but, judging from experiments conducted by Dobzhansky (1951b) using species of *Drosophila*, the frequency of inter-specific matings in confinement is almost certainly far from being a true indication of what actually obtains in nature. It is, in fact, a common experience that an inherent antipathy to

4Unfortunately no record was taken as to the 'nuptial' status of the backward *C. fumiferana* females observed in flight at McIntosh Road in 1949. According to Dobzhansky (1951b) it is extremely rare to find virgin *Drosophila* females among trapped flies, so that in this species, at least, mating must be rapidly resorted to. The possibility of virginity being a long protracted condition in *Choristoneura* is rather strictly precluded, first, by the avidity with which males approach females in cage experiments, second, by the tendency for the sex ratio among adults of both species to lean towards an excess of males, and, third, by the demonstration in cage experiments (for what it is worth) that the male is capable of successful bigamy and even trigamy. Parenthetically, it has been demonstrated by direct observation that the female can be induced to be bi-androus, but it remains to determine to what extent a second provision of sperm can be utilized. Efforts to measure this by offering *C. pinus* males to *C. fumiferana* females that had already been inseminated by conspecific males (the two types of offspring are readily distinguishable) have proved fruitless, doubtless because the reluctance of the female to engage in a second copulation is strongly reinforced by the considerable effect of sexual isolation *per se*.

TABLE IV

Mean time of occurrence of four types of matings based on daily deviations from time of first mating

Mating	No.	Mean	Mean ♀	Mean ♂
C. fumiferana ♀ x *C. fumiferana* ♂	28	2h. 33m.	2h. 43m.	2h. 56m.
C. fumiferana ♀ x *C. pinus* ♂	7	3h. 48m.		
C. pinus ♀ x *C. fumiferana* ♂	7	4h. 57m.		
C. pinus ♀ x *C. pinus* ♂	17	4h. 24m.	4h. 23m.	4h. 10m.

cross-mating breaks down under artificial experimental conditions, although proving an effective mechanism under natural conditions. This was indeed demonstrated during 1948 and 1949 at the Wabigoon River and McIntosh Road investigation sites in experiments designed to test the efficacy of sexual isolation under what approached natural conditions (30″ x 30″ x 36″ screened cages into which the two species were introduced in the frequencies and order in which they eclosed). Numerically these tests were severely restricted by the extent to which the phenological difference between the two species expressed itself. In 1948, however, nine *C. pinus* males were introduced into a cage containing 25 male and 13 female *C. fumiferana* (all previously unmated) and both males and females of the former species were added on subsequent days without cross-mating occurring. In 1949 an overlap of the two species in cage populations occupied a four-day period and again there were no hybrid unions.

Exactly what factors operate to reduce the frequency of interspecific matings in standard laboratory experiments has proved difficult to determine. The two species have courtship rituals that are alone performed by the aggressive males, the females being undemonstrative. These prologues to mating appear to the observer to be identical, and presumably are at least very similar, for hybridization occurs in cages relatively frequently. Considerable evidence has been tediously accrued that points to the existence of a difference between the two species in their intrinsic patterns of mating time, a difference which contributes in major degree to their sexual isolation. Both are predominantly crepuscular mating species, but *C. fumiferana* shows a pronounced tendency to enter copula earlier on any particular day than does *C. pinus*. The determining factor is clearly a firmly ingrained reluctance on the part of females to deviate from their inherent mating hour (Table IV). As has already been implied, males of both species respond almost immediately to the presence of females (regardless of species), but their advances are initially rebuffed by both types of females.[5] A breakdown in the resistance pattern is shown first by *C. fumiferana* females, but the breakdown is not unaccompanied by discretion, for the first unions consummated are largely with their own males, and are only later followed by mating with *C. pinus* males. Next, the *C. pinus* females start to relax their active resistance, allowing conspecific males and unmated but still demonstrative *C. fumiferana* males to enter cupola. This period of activity involves a majority of the *C. pinus* males (the remnant, unaccommodated *C. fumiferana* males being largely repulsed), and the average mating-day usually ends with sporadic matings between *C. pinus*

[5]The non-discrimination of the male is readily attested to by the observation of two instances of homosexual union in sexual isolation experiments.

females and their delinquent males and often the occasional alien male whose interests have been revived. It remains to be said that the frequencies of the four types of matings given in summary form in Table III show either that the females of the two species have equal powers of discrimination, or that they are equally bound to the differential in mating time that contributes to their partial isolation, or both.

Hybrid sterility: In hybrids produced artificially there is generally no exceptional sterility. Among the eggs laid by some of the first F_1 hybrid females obtained, a considerable degree of sterility was, however, noted: it reached some 25 per cent in certain individuals. Such sterility might have either a genic or a chromosomal basis. The chromosome complements of the two parental species were already known to be indistinguishable (see Smith, 1944, for photomicrographs), each having 2n+60 chromosomes. Examination of primary spermatocyte metaphases during gamete production in brothers of the females with abnormally high sterility disclosed the presence of a configuration of four chromosomes along with 28 bivalents, rather than the 30 bivalents characteristic of the parental species. The multiple configuration indicates that the two parents differed in that one possessed two pairs of non-homologous chromosomes that had at some prior time exchanged parts, so that in one the interchanged pairs may be symbolized as A–D and B–C and the unchanged pair in the other as A–B and C–D. In the F_1 individuals the four chromosomes, having segments in common, are liable to associate in a complex of four, or three and a univalent, or as two pairs and segregate to produce gametes carrying whole chromosome or segmental deficiencies and duplications. Such gametes, being lethal, would readily account for the sterility observed among the F_2 eggs laid by the F_1 females.

TABLE V

Incidence of genetically determined sterility between and within *C. fumiferana* and *C. pinus*

	Number of eggs		% Sterile
	Sterile	Fertile	
C. fumiferana ♀ x ♂	436	19,728	2.21
C. pinus ♀ x ♂	58	2,764	2.10
C. fumiferana ♀ x *C. pinus* ♂	0	235	0.00
C. pinus ♀ x *C. fumiferana* ♂	2	329	0.61
(*C.f.* ♀ x *C.p.* ♂) ♀ ♀	103	1,156	8.91
(*C.p.* ♀ x *C.f.* ♂) ♀ ♀	15	192	7.81

In testing the validity of this most obvious explanation, representatives of both parental species were crossed to a third type of budworm, the one that occurs on Douglas fir, *Pseudotsuga taxifolia* (Poir.) Brit., in the Rocky Mountains. If the segmental interchange interpretation is correct, only one of the two resultant F_1 hybrids should exhibit a comparable amount of sterility and the devoid of a similar structural rearrangement located elsewhere in its chromosome other should be highly fertile, providing, of course, that the western population is

complement. Surprisingly, both types of F_1 females exhibited negligible sterility and brothers of both had their 60 chromosomes regularly in pairs at melosis. Subsequent hybrids between eastern representatives of the two species failed to duplicate both the multiple configuration and the high sterility originally observed, thus showing that the segmental interchange is not diagnostic of the species differences: the translocation was therefore quite clearly a property of one of the two individuals originally mated—probably a chromosome mutation that had become to some degree established in a local population.

The assessment of genetically determined sterility is rendered extremely difficult by the concomitant occurrence of physiological sterility: most of the latter is restricted to the early and late egg clusters but groups of sterile eggs not infrequently occur in the intervening clusters, with a distribution that adequately precludes a purely genetic explanation. There is considerable evidence that inherent sterility (that remaining after the exclusion of physiological sterility) runs rather uniformly around two per cent in most populations of the two species. Eggs laid by cross-mated females are appreciably more fertile, there being usually less than about one percent inviable, but the F_1 females themselves appear to be substantially more sterile than their parental types. This increased sterility may possibly result from differences in the gene arrangements characterizing the two species, differences that segregate out to some extent during meiosis in the F_1. If this is so, one is led to assume either that there are no very extensive sequential differences between the two species, or that dissimilarities in gene arrangement that may exist are rarely brought together by crossing-over. The absence of any profound differences in their respective gene arrangements would, of course, indicate that the two species have diverged only relatively recently.

Mechanical isolation: There is absolutely no evidence that structural differences between the genitalia of the two species play any part in maintaining their independence. In fact representatives of the two, once *in copula*, appear to be perfectly adapted to each other, for the mean duration of copulation is neither longer nor shorter for hybrid unions than for intra-specific unions (see Table VI).

TABLE VI

Mean elapsed time *in copula* for four types of matings: data accumulated during various years

Type of mating	Number	Mean time
C. fumiferana ♀ x *C. fumiferana* ♂	153	4h. 40m.
C. fumiferana ♀ x *C. pinus* ♂	13	4h. 35m.
C. pinus ♀ x *C. fumiferana* ♂	11	4h. 15m.
C. pinus ♀ x *C. pinus* ♂	22	4h. 00m.

Gametic isolation and hybrid inviability: Neither of these isolating mechanisms is represented among the complex that operates in preventing the flow of genes between these two species of *Choristoneura*. That the first is inoperative is shown by the high level of hatch characteristic of eggs from cross-mated females and that the second is inoperative is proved by the fecundity of hybrid females often surpassing that of the parental species.

Discussion and Conclusions

The studies conducted by Freeman (1953) and MacKay (1953) firmly establish on the classical grounds of comparative morphology that *C. fumiferana* and *C. pinus* are "good" species, separable on the basis of adult (male) and larval structural differences. Doubtless both these authors would freely admit that such anatomical characters are of strictly limited applicability: in the final analysis, determination will continue to be based on the clear-cut colour difference noted by Graham (1935) and others familiar with the two species.

The contribution made herein is aimed not so much at ascertaining whether or not there are two species (although this was an early objective, which for some time has been considered as achieved—Smith, 1949) but primarily at determining what attributes are expressed by the two species, and the relative efficacy of these properties, in maintaining their *status quo*.

From this brief review it will be seen that in Eastern Canada geographical isolation is effective in preventing introgressive hybridization throughout large parts of the total area in which, judging from the distribution of the two complexes of host trees, the two species of budworm are manifestly allopatric. Where spatial overlaps have materialized, geographical isolation is replaced almost as effectively by temporal isolation, which results from intrinsic differences in eclosion times and development rates. Furthermore, when temporal isolation fails and small portions of the two populations occur together as adults, their strongly ingrained host preferences doubtless come into play in the preservation of the integrity of the existing genotypes. Exactly what contribution is made by this ecological factor in preventing the infiltration of genes from one species into the gene pool of the other by way of the relativety few individuals that perhaps on occasion reach maturity coincidentally, might be difficult to assess even by direct observation. The apparent total absence of obvious hybrids from the field, of course, constitutes compelling evidence that hybrids do not materialize, but this might equally well be attributed to sexual isolation.

Since it is an established fact, or *a priori* likely, that geographical, ecological, and temporal isolation are each subject to breakdown and, since one can not at present be in a position to state categorically that sexual isolation *per se* is an insuperable barrier, it becomes of immediate theoretical interest to speculate as to the relative chances of the two types of hybrids being formed and to endeavour to assess the future prospects of a hybrid colony being perpetuated.

It is apparently a matter of common experience that the males of both species reach maturity in advance of their females: insectary rearings, substantiated by laboratory tests carried out under controlled conditions, have demonstrated that the priority of the male is due to sex linkage, or sex limitation, in the rate of larval development, whereby the male pupates some two days or more in advance of the female. Surprisingly enough, this differential is reversed at pupation (Table VII), so that the female has the faster rate during the pupal stage, although never of a magnitude to compensate fully for the protracted lag during larval life. Coupled with the initially earlier spring emergence and faster overall development of *C. fumiferana* relative to *C. pinus*, this has interesting and unsuspected consequences, for the sex differential in development ensures that any overlapping of adults that may materialize shall comprise, largely if not entirely, *C. fumiferana* females and *C. pinus* males (see Table VII). What, then, are the chances of such potential hybrids being perpetuated by inbreeding and what are the chances of their new gene combinations being broken up and swamped by the genotypes of the parental populations?

TABLE VII

The correlation of development rate and sex and its reversal at pupation: *C. fumiferana* and reciprocal hybrids, Laniel, P.Q., 1948; *C. pinus*, Laboratory 1951[6].

Type	No. of days devel. to pupae				Pupa to adult		Total $\frac{♂+♀}{2}$
	N♀♀	Mean	N♂♂	Mean	♀♀	♂♂	
C. f. ♀ x *C f.* ♂	33	36.6	25	34.0	9.8	10.4	45.4
C. f. ♀ x *C. p.* ♂	37	44.8	30	36.1	10.3	10.4	50.8
C. p. ♀ x *C. f.* ♂	6	40.5	12	39.2	8.8	9.9	49.2
C. p. ♀ x *C. p.* ♂	99	50.8	133	46.3	13.3	14.2	62.3

Extensive rearing experiments have adequately established that the innate differences in tempo of development that characterize the two species are to a considerable extent sex linked, with, moreover, the faster rate of *C. fumiferana* incompletely dominant. It seems at present logical to envisage the genes primarily determining development rate as being borne on the autosomes (or, better, to constitute part of the general genetic background), with the expression of these genes being dependent on the action of an epistatic gene, or genes, located on the X chromosome. In view of this and the criss-cross manner in which the sex chromosomes are transmitted from parents to offspring, the two reciprocal F_1 hybrids show sexual differences in their rates of development: the reciprocal F_1 males have comparable rates, but their sisters differ, females from *pinus* ♀ x *fumiferana* ♂ being faster than females from *fumiferana* ♀ x *pinus* ♂. As an example, the developmental times for *C. fumiferana* and the two reciprocal hybrids, by sexes, in 1948, are given in Table VII, along with the adjusted figures for laboratory reared *C. pinus* in 1951.

The combined effect of some degree of dominance and the sex linkage of interspecific differences in development rate confers a high degree of isolation by sexes on the progeny of one of the two conceivable types of hybrids–the one that is perhaps just remotely liable to materialize in nature. Diametrically opposed to this is the strong co-ordination in eclosion of males and females from the reciprocal cross, the effect of which is to ensure their ability to inbreed –an assurance which is nevertheless nullified by the extreme improbability of their ever occurring in the wild state. The limitation imposed in the former case is illustrated graphically in Fig. 1. There, I have plotted as percentages against time the data compiled at the Wabigoon River in 1948 concerning eclosion by sexes from populations taken off white and black spruce, balsam fir, and jack pine. The two species provide distributions that illustrate: (1) the precedence of males in eclosion; (2) the general deferment of *C. pinus* as a whole; and (3) the juxtaposition of *C. fumiferana* females and *C. pinus* males. Superimposed on this graph are curves for the two sexes in the F_1 progeny from a series of crosses between *C. fumiferana* females and *C. pinus* males made in 1947 and 1948 and reared in 1948 and 1949 under insectary conditions at Laniel, P.Q. These two curves have been co-ordinated along the X-axis on the basis of the

[6]Technical difficulties in rearing *C. pinus* on jack pine foliage and the greater ease with which larvae can be cultured on balsam fir foliage deprive us of strictly comparable figures for this species. It is obviously retarded by a diet of balsam fir, but phenological observation in areas of overlap suggest that the value of 55.1 days obtained for *C. fumiferana* ♀ x *C. pinus* ♂ hybrid females is a better fit to expectation than the adjusted values given for *C. pinus*. It should be noted that little, if any, of the sexual differences between and within reciprocal hybrids is to be attributed to the cytoplasmic inheritance of development rate or to maternal diet preferences.

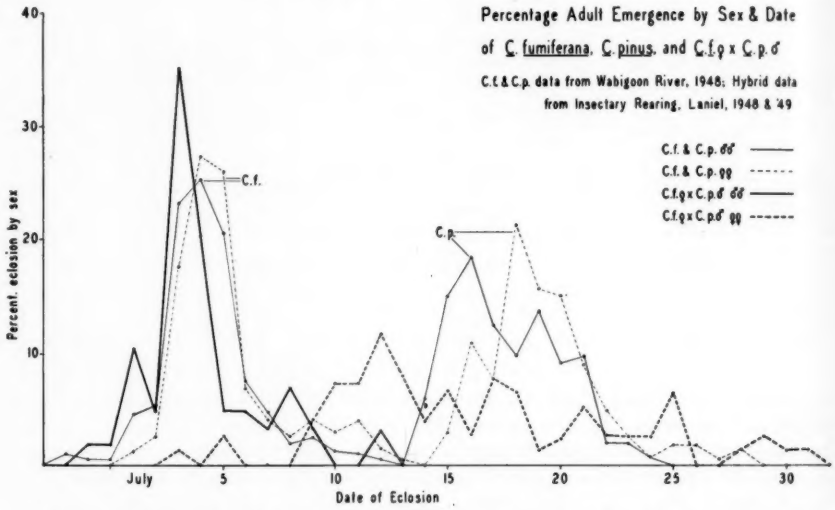

Fig. 1. Percentage plotted against time of eclosion by sexes of *C. fumiferana*, *C. pinus*, and F_1 progeny from artificial crosses between *C. fumiferana* ♀♀ *and C. pinus* ♂♂.

eclosion times of *C. fumiferana* controls reared at Laniel at the same time, the *C. fumiferana* male distribution at Laniel being fitted to that of the *C. fumiferana* male curve at the Wabigoon River.

It will be at once clear that the bulk of the hybrid males mature in conjunction with *C. fumiferana* females and that the majority of the hybrid females are deferred in eclosion until *C. pinus* males have emerged[7]. It is obvious, then, that the opportunity for such hybrids to inbreed would be severely curtailed: the bulk of the males would perforce backcross into the *C. fumiferana* population, whereas the majority of the hybrid females would of necessity backcross into the *C. pinus* population.

In contradistinction, male and female progeny from the reciprocal cross could mature together in nature, and the high frequency of brother-sister matings so assured would provide a maximum of recombination between the two original arrays of genes and hence a maximum production of both the least and most harmonious adaptive combinations for selection to act on. Clearly the more promising type of F_1 hybrid, from the point of view of evolutionary potentiality, is the one which is completely discriminated against by temporal isolation.

Hence, as a result of differences in the genetic structure of the two species, only one-way introgressive hybridization is remotely possible. Its realization would, however, give rise to two alternative channels through which a gene flown between the two species would be theoretically ensured. That hybridization does not occur in nature is made virtually certain from our knowledge of the efficacy of reproductive isolation; whether in fact it does not is for the future to decide and for population genetics to determine.

7It is of interest to note that hybrid females are more variable in their eclosion times than are hybrid males, for this is a consequence of the sex linkage of the genes governing interspecific differences in rate of development: females receive their lone X from their fathers, so that any heterozygosity of the X chromosomes in the male parent, regardless of dominance (or epistasis) and recessiveness (or hypostasis), is fully expressed in the daughters. On the other hand, males inherit an X from each parent and, because the mother can contribute but one, variability among sons is limited to that conferred upon them collectively by the Xs of the father—relative to their sex-chromosome constitution, the sons might appropriately be termed semi-identical. Variability among sons is, moreover, restricted in expression by the fact that the sex-linked development-rate genes of *C. fumiferana* are in large measure dominant to those of *C. pinus*.

Summary

Introgressive hybridization between sympatric populations of *Choristoneura fumiferana* and *C. pinus* is shown to be prevented in nature by reproductive isolation. This is a co-operative complex with ecological, temporal, and sexual components: the first is primarily a matter of host-tree preferences; the second obtains through interspecific differences in time of emergence from diapause (phenological isolation) and in rate of subsequent development (ontogenetic isolation); the third is conditioned by an innate repugnance to cross-mating expressed solely by females of both species, which is reinforced by their reluctance to deviate from a differential in mating hour.

Experiments prove that the sex-linked, species-specific development rates and the inherent tendency for males to eclose before females furnish artificially-produced reciprocal hybrids with different capacities for inbreeding. Therefore, although it is concluded that the integrity of the two species is fully maintained in nature, were reproductive isolation to break down, it is the hybrid type with the better theoretical chance of materializing that would suffer more from sexual differences in eclosion time. As a consequence, new gene arrays would be strictly limited in number and largely siphoned back into, and swamped by, the gene pools of the parental populations.

Acknowledgments

It is a pleasure to acknowledge that the observations at the Wabigoon River and McIntosh Road investigations sites were made under the supervision of H. M. Thomson of this laboratory during the course of his own pathological studies.

NOTE: At the time this paper was written in March, 1952, the only known failure of temporal isolation between adults of *C. fumiferana* and *C. pinus* was the almost negligible amount reported on herein. As stated, the *fumiferana* females were almost certainly mated before adult *pinus* males eclosed. In the early spring of 1952, doubtless owing to the unseasonably high temperatures that had prevailed, phenological isolation was found to have failed in the Kenora District of western Ontario. This resulted in a considerable overlap of virgin adults of the two species and provided an opportunity to assess the contributions made by the ecological, temporal, and sexual components to reproductive isolation. These findings will appear in the Proceedings of the Ninth International Congress of Genetics.

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Hymenopterous Parasites of *Choristoneura pinus* Free. (Lepidoptera: Tortricidae) in Canada[1]

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The following list of hymenopterous parasites of *Choristoneura pinus* Free. is based on an analysis of two collections that the writer recently received through the kindness of Dr. T. N. Freeman. The first collection consisted of 116 mature larvae and pupae of *C. pinus* taken by Dr. Freeman at Normandale (Norfolk Co.), Ont., early in July, 1951, in a plantation of *Pinus banksiana* Lamb. Rearings from this lot, at Ottawa, by Dr. Freeman and the writer yielded 48 moths and 41 specimens of parasites, the latter comprising 10 species. There was a pupal mortality of 27 specimens. The second collection consisted of 75 adult parasites that were reared at Ottawa by Dr. Freeman from a lot of 456 pupae of *C. pinus* taken by Mr. V. Hildahl at Beauséjour, Man., during July, 1951, on *P. banksiana*. There were five species of parasites in this collection, three of which are not represented in the Normandale material.

Of the 13 species of parasites in the two collections noted above, nine are recorded in the literature as parasites of *Choristoneura fumiferana* (Clem.). This is not surprising in view of the many biological resemblances between this species and *C. pinus*. It emphasizes, however, the importance of considering host relationships in any studies of these species involving problems of parasite distribution and abundance. The fact that *C. pinus* has, until recently, been more or less confused with *C. fumiferana*, and until now has not been nominally recognized, has impeded the reporting of its parasites, and it appears timely, therefore, to present the following list.

Normandale Collection

	Date(s) of emergence of adult parasites	No. of specimens reared ♂	♀
Braconidae			
**Meteorus trachynotus* Vier.	July 19	1	
Ichneumonidae			
**Scambus hispae* (Harr.)	July 16–23	2	3
**Calliephialtes comstockii* (Cress.)	July 20	1	1
**Apechthis ontario* (Cress.)	July 19		1
**Itoplectis conquisitor* (Say)	July 16–19	3	12
**Gelis tenellus* (Say)	July 20		1
Chalcidoidea (identifications kindly provided by Dr. O. Peck, Systematic Entomology, Ottawa)			
**Habrocytus phycidis* Ashm.	July 16–19	3	6
Eurytoma sp. near *atripes* Gahan	July 20		2
Brachymeria ovata (Say)	July 16–23	1	3
Spilochalcis sp. near *sanguineiventris* (Cress.)	July 20		1

Beauséjour Collection

	Date(s) of emergence of adult parasites	No. of specimens reared ♂	♀
Ichneumonidae			
**Apechthis ontario* (Cress.)	July 22	1	
**Itoplectis conquisitor* (Say)	July 17–27	13	12
**Phaeogenes hariolus* (Cress.)	July 20–Aug. 2	37	10
**Glypta fumiferanae* (Vier.)	July 24	1	
Campoplex hyalinus (Prov.)	July 29		1

*The asterisk denotes species that have been recorded in the literature as parasites of *C. fumiferana*.

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